

**AVOIDANCE OF DIRECT SUNLIGHT BY ADULT
HESPEROPSIS GRACIELAE (MACNEILL)
(LEPIDOPTERA: HESPERIIDAE)**

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Abstract.—Perched *Hesperopsis graciela* (MacNeill) adults were partially or entirely exposed to direct sunlight (solar radiation), and the response times were recorded when the skippers avoided continued exposure by flying or walking to shade. Of the skippers partially exposed to direct sunlight, those exposed only on their heads, thoraces, and basal portions of the wings sought shade earlier than those exposed only on their abdomens and distal portions of the wings. Skippers entirely exposed to direct sunlight sought shade earlier than those partially exposed to direct sunlight. Response rates (inverse of response times) of skippers partially exposed to direct sunlight, when summed, were equivalent to response rates of skippers entirely exposed to direct sunlight, inferring that thoracic and abdominal heating rates were independent and additive. Estimated thoracic ($0.6^{\circ}\text{ C}\cdot\text{s}^{-1}$) and abdominal ($0.3^{\circ}\text{ C}\cdot\text{s}^{-1}$) heating rates were comparable to those measured in other similarly-sized HesperIIDae. Results indicate that perched *H. graciela* adults rapidly increase body temperature when exposed to radiation and suggest that the species' characteristic flight within plant canopies is a thermoregulatory behavior to prevent overheating.

Key Words.—Insecta, Lepidoptera, HesperIIDae, *Hesperopsis graciela*, thermoregulation.

MacNeill's sootywing, *Hesperopsis graciela* (MacNeill), is a small (wing-spread ≈ 23 mm) dark-brown skipper (HesperIIDae; Pyrginae) found along the lower Colorado River and its tributaries in southeastern California, western Arizona, southern Nevada, and southern Utah (Scott 1986). The species' range crosses two desert biogeographic provinces, the Mohavian north of Nevada's southern tip and the Sonoran south of Nevada's southern tip (Lowe & Brown 1982). Flights of *H. graciela* occur from April to October with three generations in southern Nevada (Austin & Austin 1980) and two generations in southeastern California (April & July to October, Emmel & Emmel 1973). Larvae of *H. graciela* feed on *Atriplex lentiformis* (Torrey) (Chenopodiaceae), a shrub found in dense clumps along lower Colorado River drainages (Emmel & Emmel 1973). However, *H. graciela* is more rare than would be expected based on the occurrence of its hostplant (Austin & Austin 1980), and this rarity has afforded the skipper the global rank of 'G3?' (L. Jaress, Ariz. Game & Fish Dept., Phoenix, personal communication), indicating its conservation status is rare or uncommon but not imperiled (Master 1991).

Hesperopsis graciela's characteristic tendency of flying within the cover of riparian shrubs (MacNeill 1970) suggests the species may require shade to prevent overheating in the high insolation and summer air temperatures that prevail within its range, especially in southern Arizona and California. For example, average daily maximum air temperatures at the lower Colorado River near Parker, Arizona (weather station Parker 6 NE, lat. 34.2° N , long. 114.2° W , elevation 125 m), during 1893–1996 in July, August, and September were 42.4° C , 41.4° C , and 38.7° C , respectively (Nat. Oceanic & Atmospheric Admin., Western Regional Climate Center, Reno, Nevada). *Hesperopsis graciela* is diurnal and has been

observed flying within and between plant canopies between 0930 MST and 1330 MST during September near Parker (Wiesenborn 1997). To better understand *H. graciellae*'s affinity for plant cover, this study examines the species' avoidance of partial and entire exposure to direct sunlight and interprets the avoidance as a thermoregulatory response preventing overheating.

MATERIALS AND METHODS

The study site was located at an elevation of 150 m on the upper floodplain along the southern edge of the Bill Williams River 25 km northeast of Parker, La Paz County, Arizona, and 3 km east of Lake Havasu, a Colorado River reservoir. Principal vegetation at the site is *A. lentiformis*, *Acacia greggii* Gray, *Pluchea sericea* (Nuttall), *Cercidium* sp., *Prosopis glandulosa* Torrey, and *Salix gooddingii* Ball. *Hesperopsis graciellae* adults were individually captured with an aerial net and immediately placed into a shaded 31 cm \times 31 cm \times 31 cm aluminum-frame cage (BioQuip Products, Gardena, California). The cage was covered on the bottom and on two sides with 32-mesh plastic screen, on one side with aluminum, on the top with clear vinyl, and on one side with a cloth sleeve for inside access. The skipper was allowed to acclimate for 5 min, and the cage was repositioned with its aluminum side shaded and direct sunlight (solar radiation) transmitted through the top to illuminate one quarter of the cage bottom. A 10-cm long *A. lentiformis* branch with 4–5 leaves was placed under the skipper at the beginning of each observation. The skipper was allowed to walk or fly onto the branch and placed in shade on the cage bottom for 1 min. Skippers that flew from the branch before the 1-min shading period had elapsed were placed back onto the branch and the 1-min period repeated. The branch then was picked up and the skipper's dorsal surface subjected to one of four treatments (see Fig. 1): (1) entirely shaded (control), (2) only the abdomen and distal portions of the wings in direct sunlight, (3) only the head, thorax, and basal portions of the wings in direct sunlight, and (4) entirely in direct sunlight. The time was recorded when the treatment was begun and when the skipper flew or walked. Subtracting the former from the latter calculated the elapsed avoidance response time in seconds. Observations were stopped after 5 min if flight or walking did not occur (10 of 24 observations in the entirely-shaded treatment). Flights from, or walking on, the branch always were to shade.

Each trial consisted of each treatment performed three times on the same skipper, and the order of testing within each trial was randomized over the 12 observations. Three trials were performed on 30 Apr, three trials on 1 May, and two trials on 2 May 1997. Trials were performed under 0–5% cloud cover between 1010 MST and 1411 MST and lasted 26–54 min each. Skippers used in the first six trials were released, whereas those used in the last two trials were collected and deposited as voucher specimens at the University of Arizona Insect Museum, Tucson. Although care was taken to prevent damaging the skippers examined, some scale loss, especially from the dorsal thorax, occurred during each trial.

Meteorological measurements (range, \bar{x}) taken at the beginning and end of each trial included incident light intensity (measured with a Sekonic L-398 light meter) in direct sunlight outside (103–110, 107 kilolux [klx]) and inside (55–107, 94 klx) the cage and in shade inside the cage (5.2–24, 13 klx), relative humidity (21–36, 26%), and air temperature outside (30–38, 35° C) and inside the cage

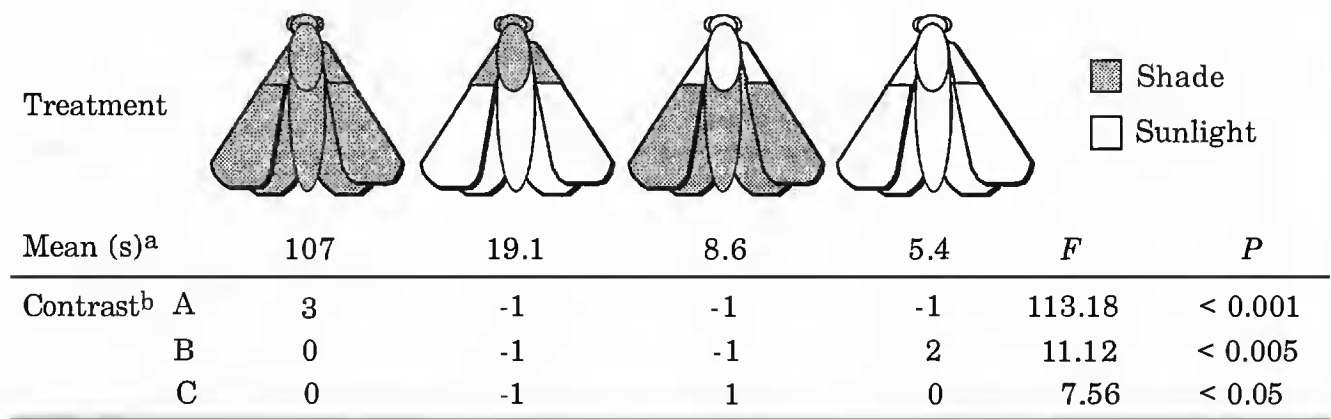
(32–40, 36° C). During each trial, air temperature was 0–2° C higher, and direct sunlight 0–52 klx lower, inside compared with outside the cage. Air temperature inside the cage at the beginning of each observation was estimated by linear interpolation between the temperatures measured at the beginning and end of each trial.

Avoidance response times were transformed $\log(Y + 1)$ and analyzed using analysis of variance with cage air temperature as a covariate, trials as blocks, and within-treatment observations in each trial as subsamples (Steel & Torrie 1980). Treatment means adjusted for the covariate were compared with orthogonal contrasts. Response rates were calculated by taking the inverse of avoidance response times averaged across subsamples in each trial. Response rates in skippers partially exposed to direct sunlight were summed (treatments [2] plus [3] above) within each trial, and these summed response rates were compared (*t*-test paired by trial) with response rates in skippers entirely exposed to direct sunlight.

RESULTS

*Hesperopsis graciela*e oriented both their front and hind wings approximately 45° below vertical during the observations and 1 min shading periods. Thus the wings received direct sunlight at more of an acute angle than did the dorsum. Skippers also periodically flexed both their front and hind wings upward, raising them to vertical and quickly lowering them back to the 45° angle; the frequency of this behavior increased during observations where skippers were exposed to direct sunlight. Flight or walking from direct sunlight also was immediately preceded by antennal movement.

Avoidance response times by *H. graciela*e were not related to cage air temperature ($F = 0.22$; $df = 1,20$; $P > 0.05$) but were different between treatments ($F = 44.0$; $df = 3,20$; $P < 0.001$) and between trials ($F = 7.92$; $df = 7,20$; $P < 0.001$). Skippers exposed to direct sunlight responded earlier than those kept in shade (Fig. 1, contrast A). Skippers entirely exposed to direct sunlight responded earlier than those partially exposed to direct sunlight (Fig. 1, contrast B). Skippers exposed to direct sunlight on their heads, thoraces, and basal portions of the wings responded earlier than those exposed on their abdomens and distal portions of the wings (Fig. 1, contrast C). Response rates of skippers partially exposed to direct sunlight, when summed ($0.21 \pm 0.16 \text{ s}^{-1}$; $\bar{y} \pm \text{SD}$), were equivalent ($t = -0.037$;



^aRetransformed adjusted means from data transformed $\log(Y+1)$; treatment SE = 0.2 s, $n = 24$.
^b $df = 1,20$.

Figure 1. Avoidance response times in second elapsed by *Hesperopsis graciela*e exposed to shade and direct sunlight.

df = 7; $P = 0.97$) to response rates of skippers entirely exposed to direct sunlight ($0.20 \pm 0.13 \text{ s}^{-1}$).

DISCUSSION

Avoidance of direct sunlight by *H. graciellae* exposed only on the abdomen and distal portions of the wings indicates skippers responded to increasing body temperature rather than visual cues. However, basking to elevate body temperature (Heinrich 1993) was not required for skippers to respond, because cage air temperatures were within the range of body temperatures (30–40° C) known to allow voluntary activity in other butterflies (*Colias* spp. [Pieridae], Kingsolver & Watt 1983). Assuming body temperatures of *H. graciellae* perched for 1 min in shade approximated mean air temperature inside the cage, and *H. graciellae* initiated shade-seeking at the same body temperatures (40–42° C) *Colias* spp. exposed to direct sunlight also seek shade (Kingsolver & Watt 1983), body temperatures of skippers increased 4.0–6.0° C during exposure to direct sunlight. This estimates heating rates of 0.47–0.70° C·s⁻¹ for *H. graciellae* exposed to direct sunlight only on the head, thorax, and proximal portions of the wings and 0.21–0.31° C·s⁻¹ for *H. graciellae* exposed to direct sunlight only on the abdomen and distal portions of the wings. For comparison, male *Thymelicus lineola* (Ochsenheimer) (Hesperiidae; Hesperinae, wingspread ≈ 26 mm, Scott 1986) exposed to radiation for 30 s at an initial air temperature of 11° C increased thoracic temperatures 0.48° C·s⁻¹ and abdominal temperatures 0.38° C·s⁻¹ (Pivnick & McNeil 1986). The similarity between heating rates estimated in *H. graciellae* and measured in *T. lineola* indicates *H. graciellae*'s avoidance of continued exposure to direct sunlight was a behavioral response to prevent overheating. Similar heating rates also suggest *H. graciellae* and the *Colias* spp. seek shade at similar body temperatures. In contrast to *H. graciellae*'s desert habitat, however, the *Colias* spp. studied by Kingsolver & Watt (1983) inhabit meadows at 1.7–4.0 km elevation in central Colorado. Thus *H. graciellae* appears not to have evolved a physiological tolerance for unusually-high body temperatures as has been observed in desert dragonflies (Polcyn 1994).

Hesperopsis graciellae's observed behavior of holding both front and hind wings 45° below vertical and periodically flexing them to vertical may have been a thermoregulatory response. Lowered wings can increase body temperature by trapping warm air beneath them (Wasserthal 1975) and by exposing more of the dorsum to radiation (Pivnick & McNeil 1986). Radiation reflected from the wings and onto the dorsum does not significantly affect body temperature (Heinrich 1990).

Differential heating between the thoraces and abdomens of butterflies exposed to radiation, as estimated in *H. graciellae* and measured in *T. lineola* (Pivnick & McNeil 1986), may be due to differences in mass, shape (affecting surface area exposed to radiation), reflectance, insulation, conduction through the exoskeleton, and convection by hemolymph. However, thoracic and abdominal heating (response) rates in *H. graciellae* did not interact, because these rates when independently estimated and combined were equivalent with those concurrently estimated. Such an interaction could result from hemolymph circulation between the thorax and abdomen, typical in moths but atypical in butterflies (Heinrich 1993). For example, Rawlins (1980) suggested that active *Papilio polyxenes* Fabr. butterflies

(Papilionidae) under heat stress can cool by circulating heated hemolymph from the thorax to the abdomen if the latter is in shade. Thoracic cooling by hemolymph circulation therefore is not evident in *H. graciellae*. This cooling mechanism also was rejected in *T. lineola*, because heating rates were similar in both live and dead skippers (Pivnick & McNeil 1986).

Being small skippers similar in size and shape, both *H. graciellae* and male *T. lineola* are susceptible to rapid increases in body temperature when exposed to radiation, especially when perched. This is likely a benefit for *T. lineola*, because this species inhabits meadows in eastern North America (Scott 1986) with comparatively cool climates. Air temperatures during field observations of *T. lineola* in July were 6–26° C, and skippers maintained body temperatures necessary for flight by frequently basking in sunlight (Pivnick & McNeil 1986). In *H. graciellae*'s environment of high air temperature and high insolation, rapid body temperature increase by exposure to radiation potentially is detrimental due to overheating. Body temperatures elevated to 45° C for 2 h were found to decrease lifespan and fecundity in *Colias* (Kingsolver & Watt 1983). Although butterflies cool convectively in flight (Heinrich 1993), the stout bodies exhibited by skippers (Scott 1986) may limit their ability to cool convectively due to high wing-loading ratios, high wingbeat frequencies, and greater heat generation by flight-muscle contraction (Heinrich 1974). High wing-loading may contribute to the fluttering, moth-like flight *H. graciellae* exhibits (MacNeill 1970). The likelihood of overheating, even during flight, therefore may be reduced by *H. graciellae* avoiding exposure to radiation and instead periodically perching or flying within the shade provided by vegetation, a thermoregulatory behavior observed in tropical butterflies (Heinrich 1972). Comparative studies with other butterfly species would help in understanding *H. graciellae*'s reliance on shade, the ecological consequences of this reliance, and the influence this behavior may have on the skipper's restricted distribution and abundance.

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